THYSANOPELTIDAE (TRILOBITA) FROM THE BRITISH DEVONIAN

By E. B. SELWOOD

CONTENTS

SYNOPSIS

A revision of the British Devonian Thysanopeltidae is made and the following species described: *Scutellum* (*Scutellum*) *costatum costatum* Pusch, *S.* (*Scutellum*) *costatum whidbornei* subsp. n., *S.* (*Scutellum*) *costatum lummatonensis* subsp. n., *S.* (*Scutellum*) *delicatum delicatum* (Whidborne), *S.* (*Scutellum*) *delicatum tigrinum* (Whidborne), *S.* (*Scutellum*) *pardalios* (Whidborne), *S.* (*Scutellum*) *flabelliferum* (Goldfuss).

With the exception of *S.* (*Scutellum*) *costatum costatum*, which is known only from Upper Devonian localities, and *S.* (*Scutellum*) *flabelliferum*, which is of Upper Couvinian age, the fauna comes principally from two localities of Givetian age, namely Wolborough Quarry (Zone of *Maenioceras molarium*), near Newton Abbot, and Lummaton Quarry (Zone of *Maenioceras terebratum*), Torquay. The Givetian material is abundant and shows considerable variability; this is described and the evidence suggests that the species represented are closely related. Two lineages are recognized within the variants of both *S.* (*Scutellum*) *costatum* and *S.* (*Scutellum*) *delicatum* from the Middle Devonian; these are distinguished by separate subspecific names.

I. INTRODUCTION

Thysanopeltid trilobites from the Middle Devonian were first noted by Phillips (1841), who referred specimens from "Newton" to *Bronteus flabellifer* Goldfuss. Later, in a major study of the Devonian faunas, Whidborne (1889*a*) included details of all species and localities then known. From material assembled principally from Chercombe Bridge and Wolborough, near Newton Abbot, and Lummaton, near Torquay, he recognized six species of which three (*Bronteus pardalios*, *B. tigrinus*, and *B. delicatus*) were new. Passing reference to Whidborne's work has been made in a number of publications on Continental faunas, but, so far as is known, no specimens have been held to be conspecific with his species. Additional records of *Bronteus* are included in the Newton Abbot Memoir of the Geological Survey (Ussher 1913).

With the exception of *Scutellum alutaceum* (Goldfuss), which is not well established, the present investigation has confirmed the diversity of species noted by Whidborne.

At the same time, it is evident that Whidborne only selected for description certain specimens which could be readily distinguished from species established earlier, and by no means fully described the variability of each species. Sufficient material is now available to permit a quantitative investigation of the variation, and the species from Devonshire are here redescribed in the light of this variation.

The terminology employed is essentially that used in the *Treatise of Invertebrate Paleontology*, (*O*) *Arthropoda* 1, but is also supplemented by that of Šnajdr (1960). The latter work (an account of the thysanopeltid fauna of Bohemia) includes an interpretation and terminology of the lateral glabellar markings, which differs from that given by R. & E. Richter and used in the *Treatise*. Šnajdr's interpretation is based primarily on the nature and evolution of the muscle impressions seen on the inner surface of the exoskeleton beneath the glabellar furrows. These details cannot be recognized on the material described, but the interpretation appears well founded and is followed here. Studies of the British material suggest that the broad (*sag.*) occipital furrow, which is common within the Thysanopeltidae, is double and contains a preoccipital glabellar lobe. This, with its implication of a hitherto unrecognized glabellar furrow, further complicates the terminological difficulties. The nomenclature for the glabellar furrows is set out below.

Richter	Šnajdr	This paper
3p	3g	4p
Supplementary groove	2g	3p
2p	1g	2p
1p		
—	—	1p (preoccipital glabellar furrow)

II. ACKNOWLEDGMENTS

I wish to thank particularly Dr. W. T. Dean, Dr. R. Goldring, and Professor S. Simpson, who read and criticized the original manuscript, and Mr. J. Saunders, technician in the Department of Geology at Exeter, who is responsible for the photographs. Dr. V. Loudon and Dr. M. Stone offered helpful advice on statistical problems.

Dr. R. C. Blackie (Royal Albert Memorial Museum, Exeter), Mr. A. G. Brighton (Sedgwick Museum, Cambridge), Dr. M. L. K. Curtis (City Museum, Bristol), Dr. W. T. Dean (British Museum (Natural History)), Dr. R. J. G. Savage (Geology Museum, Bristol University) and Dr. F. S. Wallis (Torquay Natural History Museum) kindly permitted the examination and arranged the loan of specimens in their care.

III. OCCURRENCE AND RANGE

The provenance of much of the museum material is incomplete and frequently ambiguous. However, almost certainly only four main localities are involved: Wolborough Quarry and Chercombe Bridge Quarry near Newton Abbot, and Lummaton Quarry and Barton Quarry now within Torquay. In each town con-

fusion arises because of the close proximity of the quarries and by the application of a variety of names, some of which have fallen into disuse, and others which have no precise geographical location. The principal alternatives and grid references are noted below.

1. Wolborough Quarry (SX852705) : Woolborough, Wolvery, Newton Abbot, Newton, Newton Bushell, Woolbury.

2. Chercombe Bridge Quarry (SX832711) : Chircombe, Cherecombe, Bradley Woods, Newton Bushell.

3. Lummaton Quarry (SX914665) : Happaway, St. Mary Church, Babbacombe, Lummaton-Barton.

4. Barton Quarry (SX913671) : No alternatives appear to be used.

Only two species of thysanopeltid trilobite recorded from South West England, *Scutellum flabelliferum* (Goldfuss) and *Scutellum costatum* Pusch, occur outside Britain. The former, which is characteristic of the Couvinian on the Continent, has only been identified positively by rare occurrences at Chercombe Bridge, probably from an horizon near to the Givetian/Couvinian boundary (Selwood 1965). This species represents the earliest thysanopeltid trilobite so far recognized from the British Devonian. *Scutellum costatum*, which has been recovered in considerable numbers from Wolborough, Lummaton and Barton, is relatively long ranging and continues both in Continental and British successions from the Givetian to the lower part of the Upper Devonian (*Manticoceras* Stufe). This particular species shows considerable variability and it has been found that forms closest to the original figures and descriptions are rare and recorded only from localities of Upper Devonian age (notably Ransleigh Quarry, near East Ogwell), whereas variants of the species from the Givetian at Lummaton and Wolborough are distinctive and referred to separate subspecies.

The British species of *Scutellum* are all of Givetian age, and occur within the Shell-Bed at Lummaton. The age of the Shell-Bed has been discussed by House (1963), who refers the horizon to the zone of *Maenioceras terebratum*. However, it seems that goniatites have not been identified positively from the Shell-Bed : recent collecting indicates that goniatites characteristically occur in a black bituminous bedded limestone, which appears as a faulted wedge in the quarry. Since these limestones, as well as the Shell-Bed, have yielded *Scutellum costatum lummatonensis* and *Scutellum costatum whidbornei*, there is some presumptive evidence for the contemporaneity of the two lithologies.

With the exception of *Scutellum delicatum tigrinum*, which has not been recognized, museum collections from Wolborough contain an identical thysanopeltid fauna to that from Lummaton. This particular locality has yielded goniatites (House 1963) indicating a lower horizon in the Givetian and referred to the zone of *Maenioceras molarium*.

IV. VARIABILITY

Scutellum occurs more commonly than any other trilobite in the British Middle Devonian, and museum collections contain large numbers of specimens. Within

TABLE I

		GIVETIAN			FRASNIAN	
	COUVINIAN	*C. cuspiforme*	*M. molarium*	*M. terebratum*	*P. lunulicosta*	*M. cordatum*
S. (Scutellum) costatum costatum	..	..	..	..	×	..
S. (Scutellum) costatum lummatonensis	..	..	×	×	..	..
S. (Scutellum) costatum whidbornei	..	..	×	×	..	..
S. (Scutellum) delicatum delicatum	..	..	×	×	..	..
S. (Scutellum) delicatum tigrinum	..	..	..	×	..	..
S. (Scutellum) pardalios	..	..	×	×	..	..
S. (Scutellum) flabelliferum	×	..	..	..	..	..
	Chercombe Bridge Limestone	?	Wolborough Limestone	Lummaton Limestone	Ransleigh Limestone	

Zonal range of the limestones based principally on House (1963). Possible gaps and duplications in the succession are not represented.

these collections pygidia predominate, and undoubtedly this bias reflects the relative prominence of pygidia during collection. The broad pygidia cause the rock to split readily to reveal complete specimens, whereas the more strongly vaulted cranidia and free cheeks are seldom found associated, and invariably need considerable preparation before being completely exposed.

Within the fauna, two distinct groups may be recognized : one in which the body is generally flattened and shows prominent, deeply impressed furrows on both the cranidium and pygidium, and another in which the body is highly vaulted and shows less prominent and less deeply impressed furrows. These two groups correspond in many ways to the *paliferum* and *companiferum* types of body plan described by R. & E. Richter (1934) but differ particularly in that the exoskeleton of the highly vaulted forms is neither greatly thicker than the flattened forms nor completely lacking in coarse ornamentation. The *paliferum* and *companiferum* groups are now considered to belong to different subgenera, but no such separation can be effected with the British material. Both types of body plan may be recognized amongst the variants of *Scutellum* (*Scutellum*) *costatum lummatonensis* subsp. n. and *S.* (*Scutellum*) *costatum whidbornei* subsp. n., and as such probably represent different adaptive forms within the species.

In addition to the variability noted above, it is clear from the large number of pygidia which has been assembled that there is, within each species, considerable

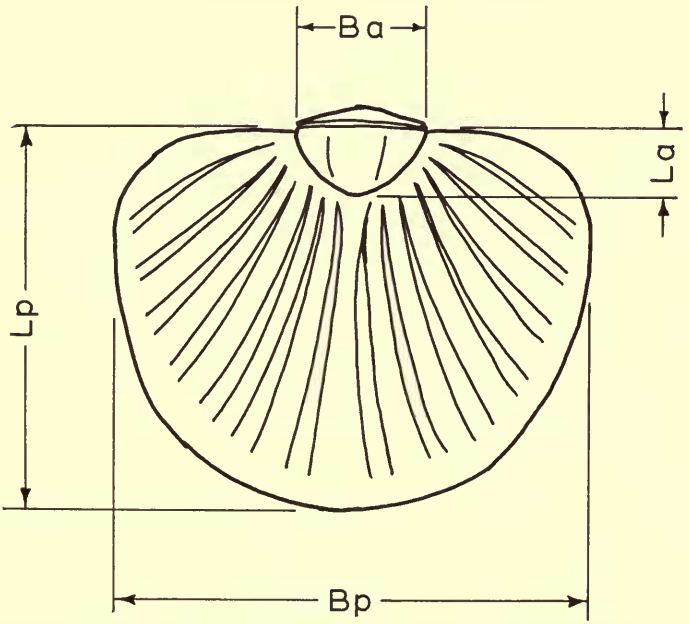
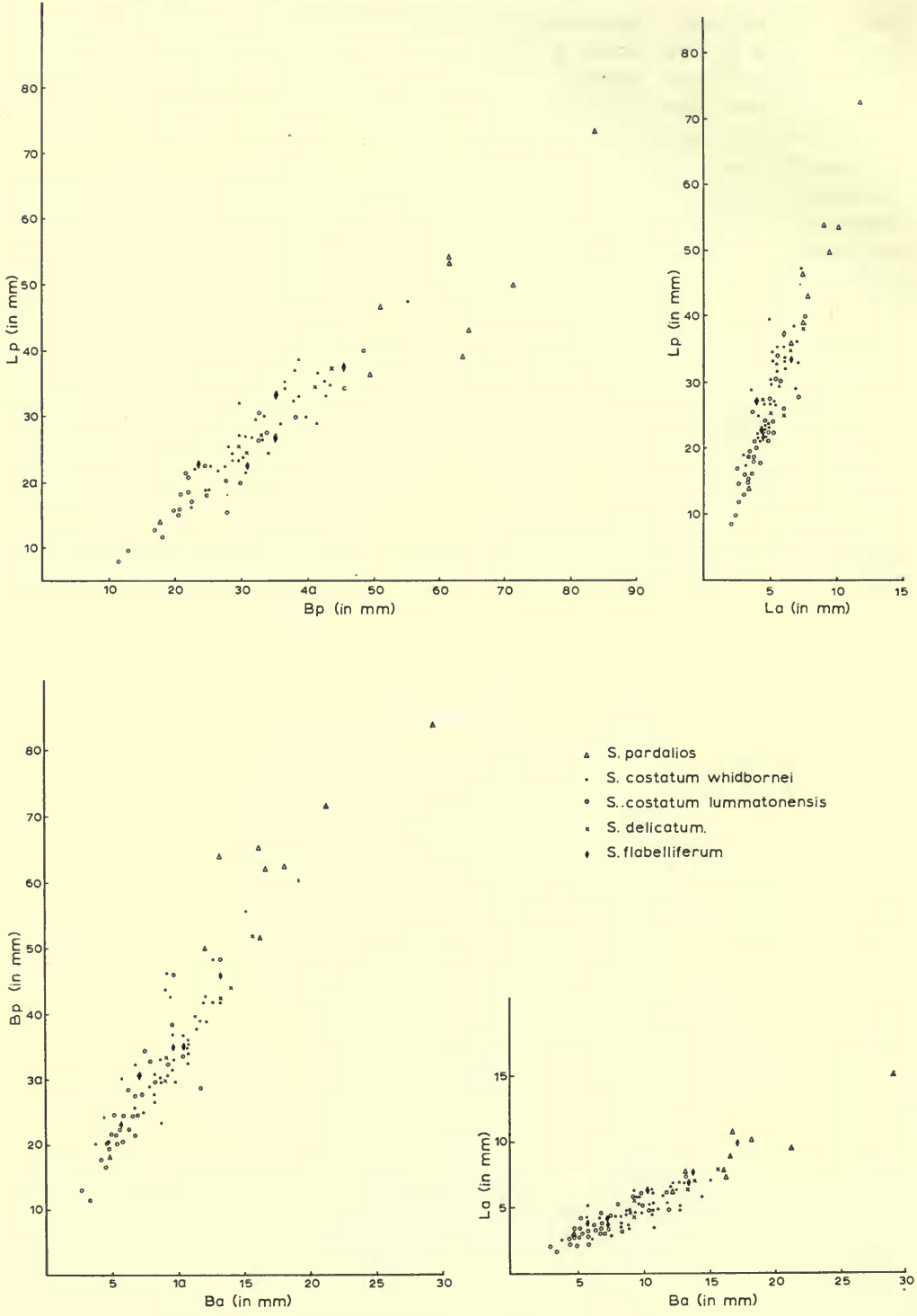


FIG. 1. Standard measurements of pygidium. *Bp*, breadth of pygidium ; *Ba*, breadth of axis ; *Lp*, length of pygidium ; *La*, length of axis. The length measurements do not include the articulating half-ring, since this delicate structure is frequently not preserved.


Lp (in mm)
Bp (in mm)
Lp (in mm)
La (in mm)
Bp (in mm)
Ba (in mm)
La (in mm)
Ba (in mm)
S. pardalios
S. costatum whidbornei
S. costatum lummatonensis
S. delicatum.
S. flabelliferum

variability of morphological features. This variability is continuous within each species recognized and extreme variants are not referred to different species.

Within the total assemblage, specimens referred to *Scutellum costatum* far outnumber all others, and when the detailed characteristics of the pygidia are examined three important trends can be recognized from a norm close to *Scutellum costatum s. str.* which lead to diverse end members. These trends may be summarized as :

(i) Trend A, which is marked by a progressive increase in prominence of the median rib and a widening of the intercostal furrows (Pl. 2, fig. 9). These specimens have affinities with *Scutellum flabelliferum.*

(ii) Trend B, in which a progressive vaulting of the dorsal exoskeleton of the pygidium is accompanied by a weakening of the intercostal furrows (Pl. 2, figs. 11, 12, 15, 16). End members are thus close to *Scutellum pardalios.*

(iii) Trend C. This is less distinctive than trends A and B, but includes a range of specimens having affinities with *Scutellum delicatum.* These specimens show an increasing prominence of the median rib but no increase in the width of the intercostal furrows.

The range in variation from specimens near to *Scutellum flabelliferum* (Trend A) through the norm to the highly vaulted forms (Trend B) is paralleled exactly by previously undescribed material in which the ribs and axes are smooth or ornamented by widely spaced granules clearly visible only under a microscope. In order to distinguish between the two lineages, the smooth range of specimens has been referred to a new subspecies, *Scutellum costatum lummatonensis,* and since none of the granulated specimens corresponds in all respects to the characteristic material described by R. & E. Richter (1926) from the Upper Devonian of Germany, these are also referred to a new subspecies, *Scutellum costatum whidbornei.*

Scatter diagrams (Text-fig. 2) relating the length of the standard measurements (Text-fig. 1) of *Scutellum costatum* show on arithmetic coordinates a markedly rectilinear distribution. This feature suggests that only a single species is present which, in the size range represented, shows isometric growth. Specimens referred to *Scutellum costatum whidbornei* are distinguished on the scatters from the subspecies *Scutellum costatum lummatonensis* and it is apparent that, whilst representatives of both subspecies are distributed throughout the range of scatters, specimens referred to *Scutellum costatum lummatonensis* are generally smaller than those of *Scutellum costatum whidbornei.* The reduced major axis has been calculated for the pairs of variables shown in Table II, and the results obtained for each subspecies compared (see Miller & Kahn 1962 : 205) by calculating the statistic Z for each pair of growth indices and referring to tables of Z which give the areas under the normal probability curve. The differences between the growth indices are not significant ($P = 0{\cdot}05$), so that the calculation fails to disprove the hypothesis tested ; namely that the difference between growth indices is no greater than would be expected by drawing two random samples from the same normal population.

FIG. 2. Scatter diagrams showing variation within British thysanopeltid trilobites.

Table II

		R.M.A.	St. Error of slope	St. Error of intercept	Dispersion around R.M.A.	Correlation coefficient	Number of specimens	Comparison of growth indices Z	Probability
Bp/Lp	a	$y = 0{\cdot}83x - 1{\cdot}14$	0·177	0·926	6·423	0·994	27	0·483	>0·05
	b	$y = 0{\cdot}92x + 2{\cdot}13$	0·016	0·850	5·487	0·995	32		
Ba/Bp	a	$y = 3{\cdot}46x + 2{\cdot}13$	0·098	1·504	7·426	0·988	30	0·054	>0·05
	b	$y = 3{\cdot}47x + 0{\cdot}05$	0·077	1·395	5·981	0·991	35		
La/Lp	a	$y = 5{\cdot}56x + 1{\cdot}35$	0·115	0·912	3·564	0·994	29	1·248	>0·05
	b	$y = 5{\cdot}30x + 1{\cdot}97$	0·176	1·755	9·144	0·980	35		
Ba/La	a	$y = 0{\cdot}51x + 0{\cdot}33$	0·013	0·213	2·413	0·998	33	0·479	>0·05
	b	$y = 0{\cdot}46x + 0{\cdot}48$	0·012	0·226	2·804	0·986	39		

a. *Scutellum* (*Scutellum*) *costatum lummatonensis*.
b. *Scutellum* (*Scutellum*) *costatum whidbornei*.

Table III

	R.M.A.	St. Error of slope	St. Error of intercept	Dispersion around R.M.A.	Correlation coefficient	Number of specimens	
Bp/Lp	$y = 0{\cdot}89x - 2{\cdot}35$	0·122	0·090	9·531	0·994	59	*S. costatum whidbornei*
Ba/Bp	$y = 3{\cdot}33x + 2{\cdot}15$	0·059	1·397	10·953	0·989	65	and
La/Lp	$y = 5{\cdot}62x - 0{\cdot}55$	0·124	1·515	11·411	0·984	64	*S. costatum lummatonensis*
Ba/La	$y = 0{\cdot}51x + 2{\cdot}19$	0·010	0·235	4·10	0·986	72	
Bp/Lp	$y = 0{\cdot}87x - 5{\cdot}75$	0·395	3·092	9·361	0·991	9	*S. pardalios*
Ba/Bp	$y = 2{\cdot}75x + 12{\cdot}73$	0·139	3·857	8·368	0·988	9	
La/Lp	$y = 5{\cdot}04x - 11{\cdot}78$	0·141	1·737	3·871	0·996	9	
Ba/La	$y = 0{\cdot}49x + 0{\cdot}46$	0·173	0·436	2·336	0·994	10	
Bp/Lp	$y = 0{\cdot}90x - 2{\cdot}64$	0·098	0·169	0·425	0·999	5	*S. delicatum*
Ba/Bp	$y = 1{\cdot}91x + 16{\cdot}34$	0·035	0·011	0·518	0·999	5	
La/Lp	$y = 4{\cdot}76x + 1{\cdot}71$	0·699	4·452	1·167	0·994	5	
Ba/La	$y = 0{\cdot}46x + 0{\cdot}67$	0·032	0·218	0·611	0·996	6	
Bp/Lp	$y = 0{\cdot}81x + 0{\cdot}57$	0·035	1·322	2·014	0·995	5	*S. flabelliferum*
Ba/Bp	$y = 2{\cdot}70x + 9{\cdot}93$	1·566	1·707	2·269	0·991	5	
La/Lp	$y = 4{\cdot}52x + 5{\cdot}27$	0·178	1·583	1·206	0·996	5	
Ba/La	$y = 0{\cdot}57x + 0{\cdot}31$	0·012	0·795	0·670	0·998	7	

Data pertaining to the other species from South West England have been added to the variation diagrams (Text-fig. 2) ; for the most part the specimens concerned either fall within, or from a natural extension of, the scatters of *Scutellum costatum*. Thus, on the basis of the measured characters, a close relationship is indicated between the species, but as a complete gradation of characters used in the original diagnoses of the species has not yet been observed, it is not permissible to conclude that the whole fauna forms part of a single species. To facilitate the comparison of the measured characters the reduced major axes of *Scutellum costatum lummatonensis* and *S. costatum whidbornei* have been recalculated as a single population and the results included in Table III together with those for *Scutellum delicatum*, *S. flabelliferum* and *S. pardalios*. When comparisons are made with *Scutellum costatum*, according to the method noted above, the results (Table IV) indicate significant ($P = 0{\cdot}05$) differences between certain pairs of growth indices. These results do not immediately mark out certain species as being similar to or different from *Scutellum costatum*, but *Scutellum delicatum*, in which only one ratio is significantly different, appears more closely related to *Scutellum costatum* than to *Scutellum pardalios* in which three of the four ratios compared are significantly different. This is in part confirmed by an inspection of other unmeasured characters, for whereas *Scutellum costatum* shows a trend towards *Scutellum delicatum*, and *Scutellum delicatum* shows both smooth and granulate forms, *Scutellum pardalios* shows limited variability only.

TABLE IV

	S. costatum/*S. pardalios*		*S. costatum*/*S. delicatum*		*S. costatum*/*S. flabelliferum*	
	Z	*P*	*Z*	*P*	*Z*	*P*
Bp/*Lp*	0·042	>0·05	0·032	>0·05	0·599	>0·05
Ba/*Bp*	3·861	<0·01	20·469	<0·01	0·403	>0·05
La/*Lp*	3·117	<0·01	1·213	>0·05	5·070	<0·01
Ba/*La*	8·245	<0·01	1·327	>0·05	1·851	>0·05

Scutellum flabelliferum is stratigraphically older than the other species but three of the four growth indices are not significantly different from those of *Scutellum costatum*. In some specimens the median rib is reduced in size and this suggests that the species could provide a range of variation from which *Scutellum costatum* could have been derived.

These comparisons thus broadly confirm the close relationship which was suggested to exist between *Scutellum costatum* and *Scutellum delicatum* and *Scutellum flabelliferum* but they do suggest that *Scutellum pardalios* is distinct. It should be remembered however that that the reduced major axes of species other than *Scutellum costatum* are based on relatively few specimens so that the calculated probabilities could well be underestimated.

V. ECOLOGY

The significance of the *paliferum* and *companiferum* types of body plan has been discussed at some length by R. & E. Richter (Richter, R. 1926 ; Richter, R. & E. 1934), who interpret certain structural elements as strengthening mechanisms for

the exoskeleton. Whilst these two types are not recognizable precisely in the terms defined by Richter within the British material, both highly vaulted and flattened forms do occur (p. 197) and these appear to have ecological significance.

In all thysanopletid trilobites the pygidium is the most prominent part of the exoskeleton, commonly equalling half the length of the body, and undoubtedly the distinctive shield-like form had considerable adaptive significance. This is confirmed by the exceptional amount of diversification within the group. The thin delicate dorsal exoskeleton, the high proportion of surface area to body volume, and the distribution of individuals through a wide range of lithologies, suggest that the flattened forms were active and free-swimming. In complete specimens it is not uncommon to find the thorax flexed so that the pygidium and cephalon are inclined in opposite directions, either upwards or downwards. Whilst this could be a *post mortem* phenomenon it is possible that swimming was aided by paddle-like movements of the pygidium. The effect of such movements would be enhanced by the considerable expansion of the pleural region. The small size of the axis and the considerable breadth of the doublure indicate that the pygidial appendages were most probably reduced; this might be expected if the swimming function had been, in part, taken over by the action of the whole pygidium. Such a reduction of the appendages would seemingly affect the efficiency of the respiratory system, but this could well be offset by direct diffusion of gases in solution through the thin integument.

The strongly vaulted forms are more robust and not so clearly adapted for active swimming. Without exception, they are all restricted to the Shell-Bed lithology at Lummaton and Wolborough, which has been interpreted by Elliot (1961) and Dineley (1961) as shell débris infillings of original depressions on a stromatoporoid reef. They may well have lived actually browsing on the reef.

VI. DETERIORATION OF THE BASAL PART OF THE GLABELLA

Within the Thysanopeltidae the "occipital furrow" is normally broad (*sag.*), deeply convex and frequently marked at the lateral extremities by tumour-like swellings. In the native British species the furrow is more deeply excavated at its anterior and posterior limits, and in *Scutellum pardalios* it shows a moderately elevated band within the furrow. This band together with the tumour-like swellings are coarsely ornamented. The presence of ornamentation within the cranidial furrows is unknown and suggests that a preoccipital glabellar lobe is present, which is divided into median and lateral lobes (the latter being represented by the tumour-like swellings). Thus the anterior excavation of the "occipital furrow" would appear to represent a transverse preoccipital glabellar furrow, the ornamented section the preoccipital glabellar lobe, and the posterior groove the true occipital furrow.

Although Whidborne fully described the character of the "occipital furrow" in his original description of *Scutellum pardalios*, no significance was attached to it by him or by later authors. A somewhat similar arrangement is also indicated in *Scutellum alutaceum geesensis* (see Richter, R. & E. 1956, pl. 7, fig. 44A) but no comment

has been offered. The present interpretation, affecting as it does the nature of the segmentation of the cephalon must be of significance and be represented in all members of the family. It is interesting to note that *Eobronteus* (Text-fig. 3A), which is usually considered to be close to the origin of the family, shows a narrow occipital furrow and, in addition, the base of the glabella is weakly constricted at its lateral margin. The latter could well indicate the presence of the basal glabellar lobe which was reduced in the course of evolution.

It is suggested therefore that the broad " occipital furrow " which is usual in the family, has a composite structure formed through the disappearance of the pre-occipital glabellar lobes and the coalescence of the preoccipital glabellar furrow and occipital furrow. Where the tumour-like swellings occur, it may be interpreted that the median glabellar lobe only has been lost.

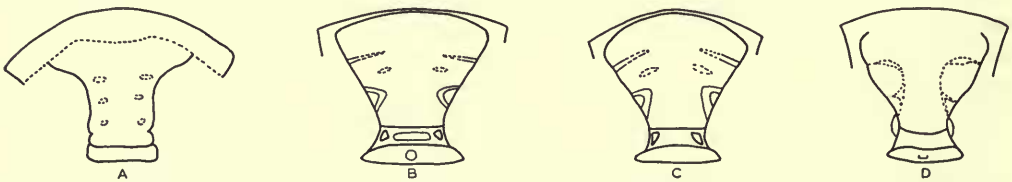


FIG. 3. Deterioration in the basal part of the glabella in the Thysanopeltidae. A, *Eobronteus laticauda* (Wahlenberg). Upper Ordovician. Occipital furrow narrow, 1p indicated at the axial furrow; B, *Scutellum* (*Scutellum*) *pardalios* (Whidborne). Middle Devonian. 1p transglabellar, preoccipital ring divided into three small lobes; C, *Scutellum* (*Scutellum*) *delicatum* (Whidborne). Middle Devonian. 1p transglabellar, median lobe of preoccipital ring absent; D, *Scutellum* (*Thysanopeltis*) *speciosum* (Hawle & Corda). Middle Devonian. Preoccipital lobes absent, a coalesced groove area only is left. (Figs. A and D after R. & E. Richter 1956).

Thus it appears that there is, within the Thysanopeltidae a deterioration of the basal part of the glabella which is quite comparable to that seen in the Phacopidae and the Proetidae (Richter, R. & E. 1939). Text-fig. 3 illustrates the principal modifications of the basal part of the glabella seen in the family; the specimens are arranged in a morphological series but this is not intended to imply stratigraphical or evolutionary significance.

VII. SYSTEMATIC DESCRIPTIONS

Family **THYSANOPELTIDAE** Hawle & Corda 1847

Genus ***SCUTELLUM*** Pusch 1833

TYPE SPECIES. *Scutellum costatum* Pusch 1833.

Scutellum* (*Scutellum*) *pardalios (Whidborne)

(Pl. 1, figs. 1–11)

1889 *Bronteus pardalios* Whidborne : 29.
1889*a* *Bronteus pardalios* Whidborne; Whidborne : 35, pl. 3, figs. 1–7.

TYPE LOCALITY. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

Lectotype. Here selected BM I.100. A pygidium figured by Whidborne (1889*a*, pl. 3, fig. 5). This figure represents a restored specimen ; the original is refigured (pl. 1, figs. 1–3).

Syntypes. SMC H.4,108–113. BM In.34924.

Figured specimens. BM IT.495 (Pl. 1, figs. 4, 5) ; BM IT.496 (Pl. 1, fig. 6) ; SMC H.4,112 (Pl. 1, fig. 7) ; RAMME 7149 (Pl. 1, figs. 8–11).

Measurements of lectotype (in mm.)

Length of pygidium	73·0	Length of axis	15·0
Breadth of pygidium	84·0	Breadth of axis	29·5

Diagnosis. A species of *Scutellum* (*Scutellum*) showing a highly vaulted, but thin, dorsal exoskeleton. Furrows, of both cranidium and pygidium less prominent and less deeply impressed than usual for subgenus. Ornament consisting of coarse, closely spaced tuberculation. On pygidium and more sporadically on cephalon, ornament developed as prominent hollow truncated cones. Median and lateral preoccipital glabellar lobes raised and ornamented. Occipital ring ornamented by a massive mesial spine.

Description

In plan the glabella is broader than it is long, and expands forward rapidly to reach a maximum breadth (2·5 times greater than at the posterior) just short of the anterior margin of the cranidium. The anterior margin of the glabella forms a broad arc which at the sagittal line extends to the anterior border. The glabellar furrows are not prominent. 4p is short, transverse and only recognizable at the lateral margin of the glabella. It deepens towards the axial furrow and is placed one-third of the distance from the anterior margin of the glabella to the preoccipital glabellar lobe. 3p is frequently scarcely recognizable, but is sometimes seen as a small transversely elliptical depression lying midway between the axial furrow and the sagittal line at a position half way between 4p and 2p. 2p is broader and more prominent than the glabellar furrows to the anterior. It is horseshoe-shaped and is marginally placed on the glabella so that the anterior and posterior branches run into the axial furrow. That part of the glabella so isolated forms a prominent node. The posterior branch is more deeply impressed than the anterior. The preoccipital furrow (1p) is transglabellar, broad (*sag.*) and deeply impressed and curves gently towards the anterior distally. It shows a symmetrical cross-section. The occipital furrow is less deeply impressed and shows an asymmetrical cross-section, rising more steeply to the anterior than to the posterior. The preoccipital glabellar lobe is low ; the median lobe is isolated and forms a narrow flat band, but the lateral lobes are more strongly elevated and recognizable as swellings arranged oblique to the preoccipital furrow. The glabella is defined by deeply impressed axial furrows ; the section that lies posterior to 2p is short and almost parallel to the sagittal line ;

it then curves sharply outwards at the occipital furrow, thus considerably increasing the breadth (*trans.*) of the occipital ring. The section of the axial furrow anterior to 2p diverges from the sagittal line at approximately 45° ; it is less deeply impressed than the posterior section and deepens towards a pit, obliquely placed across the furrow, which is positioned adjacent to glabellar furrow 4p. The occipital ring is prominent and broad, reaching half the maximum breadth of the glabella ; it is characterized by a prominent backwardly-directed mesial tubercle. The frontal area of the cranidium is small and only recognizable as slightly flattened areas situated at the anterior lateral extremities of the glabella. The anterior border furrow is weak and clearly defined only away from the sagittal line. The anterior border is narrow and shows a more or less level surface ornamented by 2–3 continuous terrace lines. From the anterior margin it is recurved sharply to the posterior ; this section is ornamented by 3–4 continuous terrace lines. At the antero-lateral margin of the cranidium this border is strongly upstanding but it is scarcely raised at the sagittal line. The fixed cheeks are large and inflated, and attain their maximum breadth posteriorly, but narrow rapidly anteriorly between the facial suture and the axial furrows. From the highest part of the fixed cheek, the cheek area falls away steeply to the posterior but more gently to the anterior. The posterior border furrow of the cranidium is positioned close to the margin. From its origin which is just removed from the axial furrow, it runs obliquely towards the anterior, making an angle of approximately 20° with the posterior border. In this section the furrow has a sharp V-shaped cross-section. At a point below the palpebral lobe the furrow turns posteriorly to run more or less parallel to the facial suture ; in this section the furrow has a broad evenly rounded cross-section. Posteriorly the furrow narrows and fails to reach the posterior margin. This furrow is not observed in the librigenae. The posterior border forms a flattened plane sloping towards the posterior border furrow ; from its origin near the glabella it widens rapidly distally. The palpebral lobe is small and semicircular in outline ; its anterior lies opposite 2p and its posterior is positioned opposite the posterior end of the glabella. The palpebral lobe is placed farther from the sagittal line than the anterior lateral border of the cranidium. The palpebral furrow forms a shallow open groove ; it has not been traced beyond the anterior limit of the lobe but continues posteriorly, progressively shallowing, following a course broadly parallel to the posterior branch of the facial suture for about one-third of the length of the latter. The anterior branch of the facial suture is long and gradually approaches the axial furrow towards the anterior. From the palpebral lobe this branch diverges outwards at approximately 10° from the exsagittal line ; opposite 3p it swings inwards but then almost immediately resumes its course to the anterior and runs more or less parallel to the sagittal line, finally cutting the anterior margin of the cephalon almost at right angles. The posterior branch of the facial suture is short, from the posterior end of the palpebral lobe it swings outwards through a semicircle to run almost parallel to the posterior border. It then curves sharply to the posterior to cut the posterior border obliquely at a distance from the axial furrow equal to four-fifths of the breadth (*trans.*) of the occipital ring.

The frontal profile is made up of 5 prominent and distinct arches comprising the central glabella, bounded by the fixed cheeks and the palpebral lobes. The glabella is strongly inflated and subtriangular in outline and its sides decline from the crest at approximately 60°. The crestal point, at the sagittal line, is rounded and lies well above the adjoining parts of the fixed cheeks. Deeply incised axial furrows separate the glabella from the fixed cheeks; these have an open V-shaped cross-section. Each fixed cheek is bounded adaxially by the axial furrow and abaxially by the palpebral furrow. The highest part of the cheek area is rounded and lies three-quarters of the distance from the axial furrow to the palpebral furrow. From this point the cheeks slope down to the axial furrow at approximately 60° and rather more gently to the palpebral furrow. The palpebral lobe is flat or gently inclined towards the weakly impressed palpebral furrow.

In side view the glabella is strongly inflated and stands well above the adjoining parts of the cranidium. It rises steeply from the preoccipital furrow and then slopes more gently to a crestal point one-third the distance from the preoccipital furrow to the anterior border. The anterior section of the curve slopes gently to the anterior but steepens up at the anterior border furrow. No preglabellar field is seen. The border furrow is evenly concave and rises anteriorly into a low insignificant border. The preoccipital furrow is relatively long (*sag.*) and deep and passes into a low evenly inflated median preoccipital lobe. The occipital furrow is narrower and less deeply impressed than the preoccipital furrow. The occipital ring is asymmetrical and rises almost vertically from the posterior to the crestal point, which approximates to the level of the base of the glabella; it then slopes more gently to the occipital furrow. The preoccipital ring is about one-third of the length (*sag.*) of the occipital ring.

The free cheek is of moderately large size and is subtriangular in outline. The eye is prominent and strongly curved longitudinally and is seen to occupy the highest part of the free cheek but lies below the level of the palpebral lobe. The eye surface is convex, directed upwards and outwards, and marked by numerous holochroal facets which give a machine turned appearance to the surface. A prominent evenly rounded eye socle separates the eye from the rest of the free cheek. The cheek area is longer than broad and slopes steeply away from the eye to a broad, concave furrow which bounds the lateral part of the cheek. Towards the anterior, the cheek area slopes more gently than laterally. The border is small and appears as a narrow rim to the cheek ornamented by discontinuous raised lines directed obliquely backwards.

In plan the pygidium is semielliptical in outline and broader than long, with a length : breadth ratio of 5 : 7; the maximum breadth is attained just posterior to the axis. The articulating half-ring is small, delicate and broadly curved. The articulating ledge which forms the inner part of the anterior margin is straight and measures three-fifths of the maximum pygidial breadth. This ledge terminates in a small articulating wing; from this point the outer part of the anterior margin curves in an even arc to the lateral margin of the pygidium. The axis is small and subtriangular. At the anterior margin its measurements exceed one-third of the

maximum breadth recorded for the pygidium and at the sagittal line it approaches one-sixth of the total pygidial length. A broad, deep and evenly rounded furrow clearly separates the axis from the articulating half-ring. This furrow is divided into three equal sections by two weak constrictions marking longitudinal furrows which are continued into the axis and effect a weak trilobation. From the anterior margin of the axis these furrows are directed posteriorly parallel to the sagittal line. At a point half the distance (*exsag.*) from the anterior margin to the axial furrow, they curve evenly inwards so that the straight sections are united by an almost semicircular furrow which, at the median line, lies only one-sixth of the total distance from the posterior margin of the axis to the anterior. The median lobe of the axis is evenly inflated and the lateral lobes slope steeply to the pleural furrows. The axial furrows are broad, smooth, and particularly deeply set at the anterior margin. At the midpoint the axial furrows are constricted ; the posterior section of each furrow makes an angle of 40° with the sagittal line whilst the anterior section, if projected, would make an angle of 50°. No segmentation of the axis has been observed. The flanks of the pygidium are strongly vaulted. The inner part of the pleural region forms a pronounced elevated platform which, at the sagittal line, extends two-thirds of the distance from the axial furrow to the posterior margin. The outer boundary of the platform crosses the ribs at their midpoints to reach the anterior margin at the articulating wing. Broadly, the platform is at two levels for ribs 1–2 lie at a distinctly lower level than ribs 4–7 ; rib 3 occupies an intermediate position. The median rib lies in a weakly depressed position on the higher platform. From the margin of the platform, the pleurae slope steeply to the periphery of the pygidium. The pleural field is divided by narrow moderately impressed intercostal furrows into 7 paired ribs and a single medianly placed rib, which radiate out from the axis. The intercostal furrows weaken towards and fail to reach the axis and also stop short of the periphery of the pygidium. The first pair of intercostal furrows is more deeply impressed than the following, so that ribs 1 and 2, and particularly rib 1, are more convex than the succeeding ribs. The two anterior pairs of intercostal furrows are almost straight but towards the posterior the furrows become weakly S-shaped, each furrow curving weakly to the anterior at the margin of the pygidium. Each rib attains its maximum breadth at the periphery and decreases in breadth progressively towards the axis. The second pair of ribs tapers very strongly and barely reaches the axis. Ribs 3–6 are moderately broad at the axis (about one-third of the maximum peripheral breadth), but rib 7 and the median rib are narrower (about one-fifth of the maximum peripheral breadth). All of the ribs are broad and flattened at the periphery but increase in convexity progressively towards the platform. On the peripheral parts of the platform the ribs are moderately inflated but, with the exception of rib 1, all flatten somewhat as the axis is approached.

In side view the axis extends posteriorly for a quarter of the total sagittal length of the pygidium ; it is strongly delimited anteriorly from the articulating half-ring by a deep evenly curved furrow and posteriorly by a less prominent groove. The axis is strongly inflated, rising steeply from the articulating furrow but descending

rather more gently to the posterior. The platform is very lightly and evenly bowed and extends posteriorly from the axis for a distance approaching two-thirds of the total post axial length (*sag.*). Posteriorly the platform passes gradually into a broadly concave slope which extends to the posterior margin of the pygidium.

Viewed from the posterior the axis occupies a prominent elevated position and appears weakly trilobed in outline. The evenly rounded median lobe of the axis passes gently into the more flattened lateral lobes ; the latter curve sharply down to deeply impressed pleural furrows. The outer section of the lateral lobe, the axial furrow, and the inner section of the anterior margin are obscured by the elevated posterior section of the pygidium, which rises in this view to a height approaching half that of the axis. The anterior pleural region is relatively low and weakly S-shaped and slopes gently to the outer margin.

The doublure is thin and is closely applied to, and follows the vaulting of, the dorsal exoskeleton. In the pygidium its inner margin reaches the platform. In the ventral view, the position of the intercostal furrows is marked by moderately convex elevations.

The anterior border of the cranidium is ornamented by 3–4 unbranched hair-like lines which run parallel to the margin of the cranidium. The posterior border of the fixed cheeks is smooth. The glabella is characterized by massive, pointed tubercles directed obliquely backwards. These tubercles, which are frequently broken, are smaller and more closely spaced towards the anterior, particularly on the median part of the glabella. Towards the posterior of the glabella the tubercles are prominent and frequently elongated transversely. In the posterior glabellar region a tubercle, larger than any of the others, lies on the sagittal line just anterior to the preoccipital furrow. Usually the occipital ring is broken medianly, but in perfect specimens it is characterized by a massive mesial tubercle which swells to occupy the whole length (*sag.*) of the ring. This tubercle is drawn out into a sturdy spine, directed obliquely backwards. The lateral parts of the ring are ornamented by small, irregular tubercles of which 2–3 would be encountered on an exsagittal traverse ; these tubercles are comparable in size to those at the anterior end of the glabella. The median lobe of the preoccipital ring is marked by two rows of small tubercles, and the lateral lobes show 2-3 tubercles of varying size. The fixed cheeks are tuberculate but with smaller tubercles than on the glabella ; these are of fairly uniform size but do increase in size slightly towards the palpebral lobe. The latter is also tuberculate and shows one particularly large tubercle on its posterior border. All of the furrows of the cranidium are smooth. The free cheek is ornamented by closely spaced tubercles comparable in size to those occurring on the outer parts of the fixed cheeks. These tubercles, which are almost invariably broken at their summits are directed obliquely backwards and become more closely spaced and regular in size towards the genal angle. Finer tubercles appear towards the borders.

The pleural region of the pygidium is bounded by a narrow margin which is ornamented by delicate hair-like lines ; at the anterior these lines run broadly parallel to the border but posteriorly lie oblique to the margin. The ribs and axis

are covered with coarse, closely spaced tubercles which appear as truncated cones directed upwards and backwards. The larger tubercles, which approach 1 mm. in diameter at their summits in large specimens, tend to be more abundant towards the periphery of the pygidium and are irregularly associated with smaller tubercles. Across the ribs (*trans.*) some 6 tubercles are recorded at the periphery and two near the axis. Inevitably many of the tubercles are damaged in the course of collecting the specimens and this gives the impression that they represent the broken bases of delicate hollow spines. However, there is a remarkable uniformity in the heights of the tubercles, which would not necessarily be expected if spines were represented as a continuation of the dorsal exoskeleton. Further, it is evident from perfectly preserved tubercles that the exoskeleton is not broken at the summit of the cone but is recurved slightly to form a narrow flat ring surrounding a depressed central area which is marked by broken secondary calcite. Thus it is unlikely the dorsal exoskeleton was ever continued into prominent spines. All of the furrows of the pygidium are smooth. Sectioned material containing pygidia embedded in matrix has revealed the presence of exceedingly delicate setae, one of which fits into the central pit of each tubercle. These setae are hollow and now filled with fibrous calcite which is apparently continuous with the secondary calcite filling the body space between the dorsal exoskeleton and the doublure. It may be presumed that the setae were movable and responsive to tactile stimuli; the extreme delicacy of the walls suggests that the setae may also have been the receptors of chemical stimuli.

The ventral surface of the doublure is ornamented by clear asymmetrical furrows which are continuous or occasionally branched and run more or less parallel to the border of the cephalon and pygidium. The furrows are crowded at the periphery but become gradually more widely spaced until at the inner margin the interval between them is six or seven times as great as at the periphery. On the dorsal surface of the doublure these furrows are represented as weakly raised areas.

Structure of the exoskeleton. All specimens possess, for their size, an exceedingly thin and delicate exoskeleton; in a pygidium 40 mm. long the total thickness is only 0·09 mm. Sectioned material reveals that the exoskeleton is made up of three layers; a thin outer (dorsal) layer, a middle layer 4 times as thick as the outer layer, and a thin inner layer twice as thick as the outer layer. The inner and outer layers are distinguished by being rather more heavily pigmented than the middle layer. This threefold division of the dorsal exoskeleton has been recorded in a number of other trilobites (Harrington 1959 : 85); in all cases the middle layer is the thickest but the relative thickness of the other layers varies. Since Kielan (1954) records that the outer layer is thicker than the inner layer in *Scutellum flabelliferum* it is evident that these relative thicknesses are not uniform for the genus.

On the cephalon the exoskeleton thins over the tubercles; it has not been possible to determine whether all of the layers are represented here, but the thickness observed suggests that more than the outer layer is represented. It is unlikely that the mineralized exoskeleton was ever continuous over the tubercles on the pygidium (p. 210).

Considering the large size of this species and the thickness of the dorsal exoskeleton it is perhaps surprising that the specimens, particularly the pygidia, have survived intact. However, R. & E. Richter (1934) have pointed out the very considerable reinforcement given by the broad doublure closely applied to the dorsal exoskeleton ; this is supplemented in *Scutellum pardalios* by thickening of the exoskeleton in the narrow furrows. Thus, the highly vaulted pygidia are supported by thickened arches (intercostal furrows) which radiate out from the axis to the periphery. The size and the general absence of malformed specimens suggest that the exoskeleton was quite adequate for its functions. Where break up of the specimens has been observed it is quite clearly posthumous and results from the effects of either compaction or tectonic activity, and reflects not the fragile exoskeleton but the large area covered by each specimen. The minor displacements associated with the fracturing of the exoskeleton frequently give the impression that the exoskeleton is thick, for it reveals beneath the true exoskeleton layers of fibrous calcite which grew around the specimen during diagenesis and appear superficially as a continuation of the dorsal exoskeleton.

Comparisons. The character of the ornamentation serves to distinguish the species from all others in the subgenus *Scutellum* (*Scutellum*). Within this subgenus the pygidium is most closely related to the highly vaulted forms of *Scutellum* (*Scutellum*) *costatum whidbornei*, but is distinguished from it by its ornament, size, and by the narrower and less clearly impressed interpleural furrows. The glabella is broader and much more strongly vaulted than in *S.* (*Scutellum*) *costatum*.

Many of the features of this species are characteristic of the subgenus *S.* (*Paralejurus*) but it is distinguished from all members of this subgenus by the thin exoskeleton, the prominent ornamentation and by the more deeply impressed intercostal furrows of the pygidium.

Scutellum (*Scutellum*) *costatum costatum* Pusch

(Pl. 2, fig. 10)

1833 *Scutellum costatum* Pusch : 119.
1926 *Scutellum costatum* Pusch ; Richter, R. & E. : 117, pl. 7, figs. 18–23 (includes earlier synonymy of the species).
1954 *Scutellum* (*Scutellum*) *costatum* Pusch ; Kielan : 31.
1955 *Bronteus costatus* (Pusch) Maksimova : 32, pl. 1, figs. 5–9.
1956 *Scutellum* (*Scutellum*) *costatum* Pusch ; Richter, R. & E. : 96, 101, pl. 2, figs. 7, 8.

Remarks. *Scutellum* (*Scutellum*) *costatum s. str.* is rare and has only been positively identified from horizons of Upper Devonian age in Devon (p. 195), and it appears to be the end member of a continuously varying series extending from the Lower Middle Devonian *Scutellum flabelliferum* through *Scutellum costatum whidbornei* subsp. n. in the Upper Middle Devonian. The possibility of such a relationship existing between *Scutellum flabelliferum* and *Scutellum costatum* was indicated by R. & E. Richter (1926 : 121).

Figured specimen. TM B.490 (Pl. 2, fig. 10).

Scutellum (*Scutellum*) *costatum whidbornei* subsp. n.

(Pl. 2, figs. 9, 11-18)

1861 *Bronteus flabellifer* Goldfuss ; Pengelly : 343, pl. 7, fig. 2.
1889*a* *Bronteus granulatus* Goldfuss ; Whidborne : 40, pl. 3, fig. 10.

Derivation of name. After the Rev. G. F. Whidborne.

Type locality. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

Holotype. BM I.5,078 (Pl. 2, figs. 17, 13).

Paratypes. BM IT.497 (Pl. 2, fig. 9) ; BM IT.498 (Pl. 2, figs. 11, 12) ; SMC H.3,778 (Pl. 2, figs. 18, 14) ; SMC H.3,782 (Pl. 2, figs. 15, 16).

Measurements of holotype (in mm.)

Length of pygidium	27·0	Length of axis	5·0
Breadth of pygidium	31·0	Breadth of axis	9·5

Diagnosis. A subspecies distinguished from *S.* (*Scutellum*) *costatum costatum* Pusch by the prominent median rib of pygidium clearly united with axis. Platform less clearly defined from rest of pleural region.

Remarks. The variability of this subspecies renders the selection of a holotype difficult. A specimen near to the norm has been chosen ; this specimen may be distinguished from *Scutellum* (*Scutellum*) *costatum costatum* by the character of the median rib as indicated in the diagnosis. Specimens which lie away from the norm inevitably show additional distinguishing features which affect the vaulting of the dorsal exoskeleton, the character of the median rib, and intercostal furrows. The changes affecting these characters are indicated on page 199.

Scutellum (*Scutellum*) *costatum lummatonensis* subsp. n.

(Pl. 2, figs. 1–8)

Derivation of name. From Lummaton, Torquay, Devon.

Type locality. Lummaton Quarry (SX914665) Torquay, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

Holotype. Pygidium SMC H.2,254 (Pl. 2, fig. 7).

Paratypes. RAMME 66/01 (Pl. 2, figs. 1, 2) ; SMC H.3,801 (Pl. 2, fig. 3) ; RAMME 66/02 (Pl. 2, figs. 4–6) ; SMC H.2,253 (Pl. 2, fig. 8).

Measurements of holotype (in mm.)

Length of pygidium	16·0	Length of axis	3·0
Breadth of pygidium	20·0	Breadth of axis	5·0

DIAGNOSIS. A subspecies of *S.* (*Scutellum*) *costatum* Pusch showing similar range of variation to *S.* (*Scutellum*) *costatum whidbornei* but distinguished by absence of all strong ornamentation.

Scutellum (*Scutellum*) *delicatum delicatum* (Whidborne 1889)

(Pl. 3, figs. 4, 7–9)

1889 *Bronteus delicatus* Whidborne : 29.
1889*a* *Bronteus delicatus* Whidborne ; Whidborne : 33, pl. 3, figs. 14, 14*a*, 15.

TYPE LOCALITY. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

HORIZON. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

LECTOTYPE. Cranidium SMC H.4,107 (Pl. 3, figs. 8, 9). Here designated.

SYNTYPES. Pygidium BM I.1,094 ; SMC H.4,106.

FIGURED SPECIMENS. BM I.1,084 (Pl. 3, fig. 4) ; SMC H.3,804 (Pl. 3, fig. 7).

MEASUREMENTS OF LECTOTYPE (in mm.)

Length (*sag.*) of cranidium	28·25	Length (*sag.*) of occipital ring	3·0
Max. breadth of glabella	26·25	Length (*sag.*) of glabella (excluding preoccipital ring)	21·5

DIAGNOSIS. A species of *Scutellum* (*Scutellum*) typically lacking coarse ornamentation. Anterior section of glabella shows pronounced asymmetrical wrinkling of dorsal exoskeleton, weakening and becoming discontinuous posteriorly. Weak elongated nodes appear in same direction along crests of wrinkles ; at first these nodes only represented along flanks of glabella but later also present medianly. Pygidium normally smooth but showing fine, widely spaced pustulation in oblique light. Pygidium characterized by prominent tumid axis weakly divided by longitudinal furrows into three lobes ; median lobe continued posteriorly into prominent undivided median rib larger than all other ribs. Intercostal furrows defining median rib frequently appearing continuous with axial furrows.

DESCRIPTION

In plan the glabella is broader than it is long, and expands rapidly forward to reach a maximum breadth (3 times that at the posterior) near to the anterior margin of the cranidium. The anterior margin of the glabella forms a broad arc reaching to the anterior border at the sagittal line. The glabellar furrows are weakly impressed, the anterior furrows only being recognizable in low, oblique light. 4p is short, transverse and forms a broad but shallow furrow extending from the axial furrow rather more than half the distance towards the sagittal line. It is most deeply impressed at its midpoint, but shallows more rapidly towards the axial furrow than towards the sagittal line. At the axial furrow it lies half the distance (*exsag.*) between the anterior of the glabella and the preoccipital glabellar furrow. 3p forms a shallow traversely elliptical depression lying rather nearer to 2p than 4p

and midway between the axial furrow and the sagittal line. 2p is broader and more prominent than the glabellar furrows to the anterior. It is horseshoe-shaped and marginally placed on the glabella so that the anterior and posterior branches run into the axial furrow; that part of the glabella, so isolated, forms a low node. The anterior branch is broader and shallower than the posterior; the latter is most deeply set at the axial furrow. The preoccipital furrow (1p) is transglabellar, deep and broad (*sag.*) and curves gently towards the anterior distally. The median preoccipital glabellar lobe is low and flattened and is inclined from anterior to posterior but scarcely rises above the preoccipital and occipital furrows. The lateral preoccipital glabellar lobes are weakly elevated and recognizable as small nodes lying oblique to the preoccipital furrow. The axial furrows are most deeply impressed posterior to 2p. Between 2p and the posterior of the glabella, the axial furrows are straight and deeply impressed and follow a course almost parallel to the sagittal line. Further to the posterior they shallow, broaden and are deflected weakly outwards at the preoccipital furrow and yet more strongly outwards at the occipital furrow, so that the occipital ring is about one and a half times the breadth (*trans.*) of the glabella posterior. Anterior to 2p the axial furrows shallow and broaden, and diverge from the exsagittal line at 45° and finally unite anteriorly with the anterior border furrow. The anterior border furrow is absent at the median line and only weakly developed at the anterior lateral termination of the glabella. The occipital ring is lens-shaped and prominent, being one and a quarter times longer (*sag.*) than the preoccipital ring. The fixed cheeks are gently inflated; at the posterior they are broad but narrow appreciably towards the anterior. The posterior border furrow is shallow and placed close to the posterior margin of the fixed cheek. The palpebral lobe is small and semicircular in outline; its anterior margin lies opposite the posterior end of the glabella and its posterior margin lies close to the posterior border furrow. At its extremity the palpebral lobe is farther from the sagittal line than any other part of the cranidium. The anterior branch of the facial suture is long and straight. From the anterior end of the palpebral lobe this branch diverges at approximately 10–15° from the exsagittal line and cuts the anterior border close to the axial furrow. The posterior branch of the facial suture is short and swings outwards through a semicircle from the posterior end of the palpebral lobe, to run almost at right angles to the sagittal line. On the line (*exsag.*) of the outer part of the palpebral lobe the suture curves sharply to the posterior to cut the posterior margin three-fifths of the distance from the axial furrow to the genal angle.

Viewed from the front the whole cranidium forms a broad, moderately inflated curve which is broken into 3 sections by the axial furrows into a central glabellar region bounded by the fixed cheeks. The glabella forms a broad, low curve sloping gently away from the crestal point at the sagittal line towards the axial furrows which, in this view, do not appear to be strongly impressed. The palpebral lobe is small and is differentiated from the rest of the fixed cheek only by being slightly more elevated; it rises distally to the height of the crest of the glabella The palpebral furrows are not recognizable. The palpebral lobe and fixed cheek slope

gently towards the axial furrow, but dip down rather more steeply at the furrow itself. The combined breadth (*trans.*) of the palpebral lobe and fixed cheek is greater than that of the glabella.

In side view the glabella is low and scarcely rises above the level of the highest parts of the fixed cheeks. The curve of the glabella forms a low flattened arc which rises very slightly from the shallow preoccipital furrow, then slopes gradually to the anterior. Two-thirds of the distance from the posterior of the glabella to the anterior the gradient increases so that the anterior of the glabella forms a more steeply inclined arc. No preglabellar field is apparent. The anterior border is low and insignificant. The preoccipital furrow is shallow and the median lobe of the preoccipital ring is scarcely recognizable ; in this view it is seen only as a gently inclined surface sloping from the occipital furrow to the preoccipital furrow. The occipital ring is prominent rising above the level of the posterior end of the glabella at its crestal point. The occipital furrow is only weakly impressed.

The free cheek is large and subtriangular in shape and is most probably continued postero-laterally into a short, sharp genal spine. The eye is prominent and is strongly curved longitudinally and is elevated to form the highest part of the free cheek, rising to a level equal to half the height of the glabella. The eye surface is convex and marked by many holochroal facets ; it rises steeply from a narrow flattened platform but is separated from it by a weak eye socle. The cheek area is longer than broad and slopes steeply, in an even curve, away from the platform to a broad but shallow lateral border furrow. The lateral border is insignificant and appears as a thin raised area. The posterior border furrow is absent.

In plan the pygidium is semielliptical in outline, being broader than it is long with a length : breadth ratio of 4 : 3. The maximum breadth is attained just anterior to the posterior termination of the axis. The articulating ledge which forms the inner part of the anterior margin is straight and measures approximately one-fifth of the maximum pygidial breadth. This ledge terminates in a small articulating wing, from this point the outer part of the anterior margin curves in an even arc to reach the lateral margin at the point of maximum breadth. The articulating half-ring is broad (*trans.*) and short. The axis is small and subtriangular in outline. At the anterior margin its measurements exceed one-third of the maximum breadth of the pygidium and at the sagittal line it approaches one-fifth of the total pygidial length. The axis is separated from the articulating half-ring by a deep, moderately broad, furrow which is arched forwards medianly and, to a lesser extent abaxially. The axial furrows are narrow and not deeply impressed. The axis is strongly inflated and faintly trilobed. At the anterior border the axis is divided into 3 approximately equal sections by 2 weakly impressed furrows ; these are continued posteriorly broadly parallel to the sagittal line. At the posterior extremity of the axis, the median lobe is of the same breadth as the median rib. The median lobe of the axis is uniformly rounded and the lateral lobes triangular in outline and they become somewhat flattened at the lateral border. The posterior termination of the axis is rounded.

The axial furrows are broad and smooth but not deeply impressed so that they are

scarcely marked at the posterior termination of the tail. The central section of the furrows is straight and would, if projected, make an angle of 45° with the sagittal line. Anterior from this central section, the furrows curve outwards rather more gently and posteriorly the axial furrows become continuous with the furrows defining the median rib. No segmentation of the axis has been observed. The pleural region forms a low flattened surface sloping gently away from the low platform bounding the axis. The junction between the platform and the rest of the pleural region is perfectly gradational. The pleural region is divided by narrow deeply impressed intercostal furrows into 7 paired ribs and a single median rib. Paired ribs 1 and 2 are straight and radiate out from the axis. The remaining ribs are gently curved ; from the axis they are directed to the posterior, broadly parallel to the sagittal line, and then sweep posteriorly outwards towards the periphery. All of the intercostal furrows fail to reach the periphery of the tail and, with the exception of those defining the median rib, all furrows weaken towards and fail to reach the axial furrows. Towards the axis the intercostal furrows are deep and have evenly rounded bottoms but, as the furrows broaden towards the periphery, they flatten to reach a maximum of one-quarter of the breadth (*trans.*) of the adjoining ribs. With the exception of the median rib all of the ribs decrease evenly in size from the periphery towards the axis and at the same time the cross-section of the ribs changes from broadly arcuate to convex. At the axis the ribs are a quarter to one-fifth of their width at the periphery. Rib 2 lies between strongly converging intercostal furrows and does not reach so far towards the axis as the adjoining ribs. The median rib is larger than any of the paired ribs ; it is bottle shaped and continuous with the axis.

In side view the axis extends posteriorly for rather less than one-quarter of the total sagittal length of the pygidium and is strongly delimited anteriorly from the articulating half-ring by a deep, evenly rounded furrow. Posteriorly it passes, without a break, into the pleural area. The articulating half-ring is small, at the sagittal line extending anteriorly for a distance equal to the maximum breadth of the articulating furrow. The axis is inflated but somewhat flattened ; it rises steeply from the articulating furrow and then flattens ; the posterior two-fifths of the axis forms a broad arc descending from the flattened area. The platform is flattened to very gently convex, and extends posteriorly for a distance of seven-twelfths of the total post-axial length (*sag.*) and then passes through a gentle curve into a broadly concave slope extending to the posterior margin of the pygidium.

Viewed from the posterior the axis occupies a prominent position and shows a weakly triangular cross-section but is weakly constricted at the midpoints of the slopes away from the sagittal line. The pleural region forms a broad low arc. The platform slopes gently from the axis to its periphery, where it curves in a broad concave slope to the margin of the pygidium. The proximal sections of ribs 1 and 2 are obscured by the slightly more elevated posterior section of the pygidium.

The doublure is broad and very thin and extends more than two-thirds of the distance from the margin of the pygidium to the axis. It is closely applied to the dorsal section of the exoskeleton and ornamented by delicate finely branched terrace

lines which run more or less parallel to the border of the pygidium. The spacing of the terrace lines increases towards the axis.

The anterior section of the glabella is ornamented by prominent asymmetrical wrinkles, which represent infoldings of the whole exoskeleton. These are continuous and run more or less parallel to the anterior border of the glabella. Towards the posterior the wrinkling weakens and becomes discontinuous, and at the same time low elongated elevations, which first appear on the lateral flanks of the glabella, become evident along the wrinkle lines. This ornamentation is represented over the whole of the posterior half of the glabella. The posterior parts of the fixed cheeks show a low irregularly spaced granulation but the anterior parts are smooth. The ornamentation of the occipital ring is imperfectly known, but the lateral parts appear to be ornamented by low elongated elevations which are broadly convex to the anterior and lie oblique to the transverse line. The anterior border is ornamented by up to 3 terrace lines.

The pygidium is smooth but in oblique light small irregularly spaced hollow pustules are discernible. It appears that the exoskeleton represented over the pustules is much thinner than that over the rest of the pygidium, so that it becomes transparent and reveals the secondary calcite filling the pustule. All of the furrows on the cranidium and pygidium are smooth.

Scutellum (*Scutellum*) *delicatum tigrinum* (Whidborne)

(Pl. 3, figs. 5, 6, 10–12)

1889 *Bronteus tigrinus* Whidborne : 34, pl. 3, fig. 12.
1889*a* *Bronteus delicatus* Whidborne ; Whidborne, pl. 3, fig. 13.
1889*a* *Bronteus granulatus* Goldfuss ; Whidborne, pl. 3, fig. 8.

Type locality. Probably Lummaton Quarry (SX914665) Torquay, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras terebratum.*

Lectotype. BM In.34923 (Pl. 3, fig. 11). Here designated.

Syntype. SMC H.2241. This cranidium is imperfectly preserved and cannot be referred to any species with certainty.

Figured specimens. SMC H.3,785 (Pl. 3, fig. 5) ; BM In.58,998 (Pl. 3, fig. 6) ; BM IT.499 (Pl. 3, fig. 10) ; BM In.34,923 (Pl. 3, fig. 11) ; SMC H.4,106 (Pl. 3, fig. 12).

Measurements of lectotype (in mm.)

Length (*sag.*) of cranidium	18·0	Length (*sag.*) of occipital ring	2·0
Max. breadth of glabella	19·0	Length (*sag.*) of glabella (excluding preoccipital ring)	12·75

Diagnosis. A subspecies of *Scutellum* (*Scutellum*) *delicatum* (Whidborne) distinguished from type species by coarser ornamentation of dorsal exoskeleton. Ornamentation consists of moderately fine granulation of ribs and axis of pygi-

dium, and moderately pronounced granulation of posterior parts of glabella. Glabella broad, showing maximum length : maximum breadth ratio of 2 : 3.

Remarks. Whidborne (1889*a*) established the species *Bronteus tigrinus* on the basis of two cranidia only and distinguished it from *Bronteus delicatus* by the broader glabella and by the presence of prominent pits within the axial furrows. Recent collecting has revealed additional material including an almost complete specimen from which it is apparent that the pygidium, like the cranidium, is closely comparable to that of *S.* (*Scutellum*) *delicatum*. However, it is distinguished quite clearly by a moderate granulation of the dorsal exoskeleton. This granulation is more closely spaced and prominent on the axis than on the ribs. In addition, the axis is less tumid and its threefold longitudinal division is more marked than in *S.* (*Scutellum*) *delicatum*. The ornamentation of the cephalon is also distinctive ; the anterior part of the glabella is characterized by a weak wrinkling giving a broadly continuous series of lines at the anterior margin. These become less prominent and more discontinuous towards the posterior. Small transversely elongated tubercles arise from the lines at the antero-lateral parts of the glabella ; these increase in prominence towards the posterior and come to occupy the whole of the posterior section of the glabella. At the same time the tubercles become less clearly elongated and appear as rounded bosses at the glabella posterior. The occipital ring is more finely ornamented than the posterior parts of the glabella, but does show a large prominent mesial tubercle. With the exception of the anterior parts, the fixed cheeks are moderately strongly granulated. The free cheeks appear to be ornamented only by light irregular wrinkling of the dorsal exoskeleton.

Whidborne's two species are thus distinguished primarily by differences in ornamentation ; *Bronteus delicatus* being smooth and *Bronteus tigrinus* granulated. This situation is paralleled exactly by the British Middle Devonian forms of *Scutellum costatum*. It appears therefore unwise to attribute more than subspecific significance to the differences in ornamentation and it is proposed to distinguish the granulated form as *S.* (*Scutellum*) *delicatum tigrinum* and the smooth form as *S.* (*Scutellum*) *delicatum delicatum*. The possibility of the two forms being varieties of the same species was envisaged by Whidborne (1889*a* : 34).

The separation of the two subspecies on the basis of the ornamentation necessitates the inclusion of one of the specimens (SMC H.4,106) figured by Whidborne (pl. 3, fig. 13) as *Bronteus delicatus* within the subspecies *S.* (*Scutellum*) *delicatum tigrinum*. The re-allocation of this specimen then allows a further distinction to be drawn ; namely that the glabella of the subspecies *tigrinum* shows a maximum breadth : maximum length ratio of 3 : 2, which is appreciably greater than in the subspecies *delicatum*.

A fairly complete specimen of this species (BM IT.499, Pl. 3, fig. 10) shows that 10 uniform segments are present in the thorax. The axis of each segment is broad, but narrower than each pleura, and forms a broad subtriangular arch rising sharply from the flattened pleural areas. Each ring is convex in section and slopes more gently towards the anterior than to the posterior, and is continued anteriorly into a broad (*trans.*) but short (*sag.*) articulating half-ring. The axial furrows are not

prominent. The proximal parts of the pleurae show evenly convex median sections which bear narrow flattened anterior and posterior articulating flanges. The distal sections of the pleura are not known.

COMPARISONS. *S.* (*Scutellum*) *delicatum* is most closely related to *S.* (*Scutellum*) *costatum* but is distinguished from it by the absence of coarse ornamentation and by the prominent tumid axis and median rib on the pygidium.

Scutellum (*Scutellum*) *flabelliferum* (Goldfuss)

(Pl. 3, figs. 1–3)

1839 *Bronteus flabellifer* Goldfuss : 361, pl. 33, fig. 3*a* (excluding pygidium), 3*c*.
1954 *Scutellum* (*Scutellum*) *flabelliferum* (Goldfuss) ; Kielan : 28, pl. 4, figs. 6–9, text-figs. 20–23 (includes earlier synonymy of the species).
1955 *Bronteus* (*Bronteus*) cf. *flabellifer* Goldfuss ; Maksimova : 43, pl. 1, figs. 2, 3.
1956 *Scutellum* (*Scutellum*) *flabelliferum* (Goldfuss) ; Richter, R. & E. : 96, pl. 7, figs. 40–42.

REMARKS. Whidborne (1889*a*) and R. & E. Richter (1925) correctly pointed out that because of confusion over specimens figured by Goldfuss (1839, 1843) many specimens from Devon ascribed to this species are properly placed in *S.* (*Scutellum*) *costatum* Pusch (= *Bronteus granulosus* Goldfuss). *Scutellum flabelliferum* is of rare occurrence and has only been identified from the Chercombe Bridge Quarry where it occurs in a black limestone in association with *Dechenella* (*Dechenella*) *setosa*, Whidborne. The preservation of this material is, in some cases, particularly good ; one large pygidium (Pl. 3, fig. 2) shows delicate tooth-like extensions arising from the anterior-lateral border. The median rib of the specimen figured by Whidborne (here re-figured : Pl. 3, fig. 3) is unusual for the species for it has the form more characteristic of *Scutellum costatum*. The presence of this variant within the assemblage tends to confirm that the latter species was derived from *Scutellum flabelliferum*.

VIII. REFERENCES

DINELEY, D. L. 1961. The Devonian system in South Devonshire. *Fld. Stud.*, London, **1** : 121–140.

ELLIOTT, G. F. 1961. A new British Devonian alga, *Palaeoporella lummatonensis*, and the brachiopod evidence of the age of the Lummaton Shell-Bed. *Proc. Geol. Ass. Lond.*, **72** : 251–260, pls. 9–10.

GOLDFUSS, A. 1839. Beiträge zur Petrefaktenkunde. B. Beiträge zur Familie der fossilen Crustaceen. *Nova Acta Acad. Caesar. Leop. Carol.*, Halle a.S., **19** : 353–364, pl. 32.

—— 1843. Systematische Übersicht der Trilobiten und Beschreibung einiger neuen Arten derselben. *Neues Jb. Min. Geol. Paläont.*, Stuttgart, **1843** : 537–567, pls. 4–6.

HARRINGTON, H. J. 1959. General description of Trilobita. *In* R. C. Moore (editor), *Treatise on Invertebrate Paleontology-O, Arthropoda 1.* (*Trilobitomorpha*). xix + 560 pp., 415 figs. Lawrence & Meriden.

HAWLE, I. & CORDA, A. J. C. 1847. *Podrom einer Monographie der bohmishen Trilobiten.* 176 pp., 7 pls. Prague.

HOUSE, M. R. 1963. Devonian ammonoid successions and facies in Devon and Cornwall. *Quart. J. Geol. Soc. Lond.*, **119** : 1–27, pls. 1–4.

KIELAN, Z. 1954. Les Trilobites mésodévoniens des Monts de Sainte-Croix. *Palaeont. polon.*, Warsaw, **6** : 1–50, pls. 1–7.

MAKSIMOVA, Z. A. 1955. Trilobity srednego i verkhnego devona Urala i severnykh Mugodzhar. *Trud. vsesoyuz. nauch.-issled. geol. Inst.*, Moscow (n.s.) **3** : 1–244, pls. 1–18.

MILLER, R. L. & KAHN, J. S. 1962. *Statistical Analysis in the Geological Sciences.* xiii + 483 pp. New York & London.

PENGELLY, W. 1861. On the Devonian age of the World. *The Geologist*, London, **4**, 332–347, pl. 7.

PHILLIPS, J. 1841. *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset.* xii + 231 pp., 60 pls. London.

PUSCH, G. G. 1833. *Geognostische Beschreibung von Polen, so wie der übrigen Nordkarpathenländer*, **1** : 338 pp. Stuttgart & Tübingen.

RICHTER, R. 1926. Von Bau und Leben der Trilobiten IV. Die Versteifungen der Schale und deraus hervorgehende Konvergenzen. *Pal. hungarica*, Budapest, **1** : 90–108.

——R. & E. 1925. Unterlagen zum Fossilium Catalogus, Trilobitae III. *Senckenbergiana*, Frankfurt a. M., **7** : 239–244.

—— 1926. Die Trilobiten des Oberdevons. *Abh. preuss. geol. Landesanst.*, Berlin (N.F.) **99** : 1–314, 12 pls.

—— 1934. Missbildungen bei Scutellidae und konstruktive Konvergenzen *Senckenbergiana*, Frankfurt a. M., **16** : 155–160.

—— 1939. Ueber *Namuropyge* n.g. und die Basisolution der Trilobiten Glatze. *Bull. Mus. R. Hist. nat. Belg.*, Brussels, **15**, 3 : 1–29.

—— 1956. Grundlagen für die Beurteilung und Einteilung der Scutelluidae (Tril.). *Senck. leth.*, Frankfurt a. M., **34** : 79–124, pls. 1–7.

SELWOOD, E. B. 1965. Dechenellid trilobites from the British Middle Devonian. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.*, London, **10** : 319–333, 1 pl.

ŠNAJDR, M. 1960. Studie o čeledi Scutelluidae (Trilobitae). *Rozpr. geol. Úst. čsl.*, Prague, **26** : 1–264, pls. 1–36.

USSHER, W. A. E. 1913. The Geology of the Country around Newton Abbot. *Mem. Geol. Surv. U.K., London.* vi + 149 pp., 3 pls.

WHIDBORNE, G. F. 1889. On some Devonian Crustacea. *Geol. Mag.*, London (3) **6** : 28–29.

—— 1889*a*. A monograph of the Devonian fauna of the South of England. Vol. 1. The fauna of the Limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh, Pt. 1 : 1–46, pls. 1–4. *Palaeontogr. Soc.*, [*Monogr.*], London.